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TEOSINTE INTROGRESSION IN THE MAIZE OF THE NOBOGAME VALLEY

BY

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> Around Nobogame grows a plant called *maizillo*, or *maizmillo*. It is more slender than the ordinary corn-plant and the ears are very small. It grows among the corn and has to be weeded out, as it injures the good plants. However, several Mexicans assured me that, when cultivated, the ears develop. After three years they grow considerably larger and may be used as food. A man in Cerro Prieto raises this kind only: others mix it with the ordinary corn. I was told that people from the Hot Country came to gather it, each taking away about one almud to mix with their seed corn. The combination is said to give splendid results in fertile soil.
>
> LUMHOLTZ, *Unknown Mexico*
> 1902

The Nobogame Valley is an isolated valley in the Sierra Madre Occidental of Mexico, and the description by Lumholtz written over fifty years ago is an accurate account of present day hybridization of teosinte with maize.

This valley, inhabited by Tarahumare Indians and Mexicans, is approximately eight miles north of the old mining town of Guadalupe y Calvo in the southwestern corner of the state of Chihuahua. Most of the valley floor is given over to the cultivation of maize, beans and squash or grazed, but teosinte does occur and is often abundant along the margins of maize fields or in the willow thickets bordering the streams. The distribution

of teosinte is limited to probably not more than 25 square miles of the valley between the elevations of 1720 and 1920 meters.

The local inhabitants recognize teosinte as distinct from maize and call it *maicillo* or *maíz sílvestre*. They are also familiar with the maize×teosinte hybrids and universally will claim that if the hybrid is cultivated for three years it produces maize. Some feel that hybridization even improves the maize.

Factors limiting gene exchange

Both teosinte and maize are wind-borne, cross-pollinated plants, and the prevention of hybridization with subsequent genetic exchange between the two species is dependent on (1) the spatial isolation of the two species, (2) the seasonal isolation of the two species, (3) the lack of fitness of the hybrid, and (4) the types of selection operating on the two parental populations.

The most effective isolating mechanism in most areas where teosinte and maize are sympatric has been the mean mid-flowering date, with maize flowering 2–5 weeks ahead of teosinte. Nobogame teosinte is unique in that it is the only teosinte population found in a habitat other than a cultivated field which is not seasonally isolated from maize. Maize of the Nobogame Valley is a five month type belonging to the race Cristalino de Chihuahua which is planted in May and harvested in September before the early killing frost. Both teosinte and maize reach mid-flowering in August.

Hybridization at Nobogame

In all the areas of both Guatemala and Mexico where teosinte and maize occur together there is some evidence (only a single F_1 hybrid in some cases) of hybridization, but never has the author found such a large number of hybrids and clear and unmistakable effect of teosinte in-

Plate LXXV

Maize of the Nobogame Valley. Cristalino de Chihuahua is a poorly defined race in Mexico which is typically a dent corn. There is considerable variation from field to field and very hard flinty kernels are frequent in the region where hybridization with teosinte occurs. 2/5 actual size.

trogression in maize cobs as exists in Nobogame. The abundance of F_1 hybrids is comparable to Chalco, where several researchers have studied maize×teosinte hybrids (López y Para (1908), Collins (1921), Bukasov (1926, 1930), Mangelsdorf (1952), and Wilkes (1967)). Unlike the region around Chalco, however, teosinte is not limited to the cultivated fields. Teosinte also occurs in dense stands along the streams and in areas protected from grazing on the surrounding hills.

Although all the fields had been harvested at the time of the field work (November), careful investigation indicates that maize×teosinte hybrids are present in the fields proper, but not as abundant as they are on the margin of the maize fields or in the willow thickets along the stream. When maize×teosinte hybrids are encountered in the maize fields of Mexico, it is usually presumed that they are from teosinte fruit-cases containing hybrid seed which were naturally disseminated in the field. In Nobogame, the female parent of the teosinte× maize hybrids is sometimes maize and thus the hybrids are often planted in the field.

Teosinte introgression

The evidence of teosinte introgression into maize is clearly seen in maize cobs throughout those parts of the valley where teosinte is most abundant. At harvest time the entire ear is brought to the granary, and for several weeks thereafter the ears are left to air dry in large piles around the courtyard. A sector of each of twenty piles representing twenty distinct fields of eight cultivators was studied. Twenty-five cobs were separated from the pile and shelled. Approximately $\frac{1}{4}$ of all the cob samples expressed the tripsacoid characteristic of a pronounced induration of the rachis and lower glume. All of the piles possessed tripsacoid cobs (Wilkes, 1968), although

a few of the samples were free of tripsacoid cobs.

Two of the fields where tripsacoid cobs had been harvested were visited and teosinte was found to be abundant around the field margin. Although most of the teosinte plants had dispersed their seed and were dried and broken, several F_1 hybrids were located which still possessed intact cobs. In one field, two teosinte backcross progeny of the F_1 maize$\times$teosinte hybrids were discovered, indicating that there is some reciprocal introgression.

Despite the presence of reciprocal introgression, most of the gene flow is from teosinte to maize. Teosinte is a wild plant possessing the ability to disperse its seed as single rachis segments, while domesticated maize has a massive cob tightly enclosed by a husk system. Only those teosinte backcross segregates which possess the genetic control for a disarticulating rachis are able to disperse their seed. This factor is primarily responsible for the unidirectional flow of genetic material. The backcrosses to teosinte that segregate a more maize-like cob with non-disarticulating rachis disperse the entire spike as a whole. The numerous seed all germinating still attached to the cob are so crowded that they either choke each other out or develop into numerous spindly plants that fail to flower. In both cases, the genetic inheritance of the maize-like cob is lethal to a plant dependent on natural dispersal of its seed for survival. The selection for the disarticulating teosinte pistillate spike and distribution of single seeds protected by a rachis-segment, along with a large population of wild plants in the surrounding region, appears to act against the effects of maize introgression on the pistillate spike of teosinte.

Study of maize ears

The evidence for introgression of tripsacoid characters from teosinte is objectively measurable in the morpholo-

PLATE LXXVI

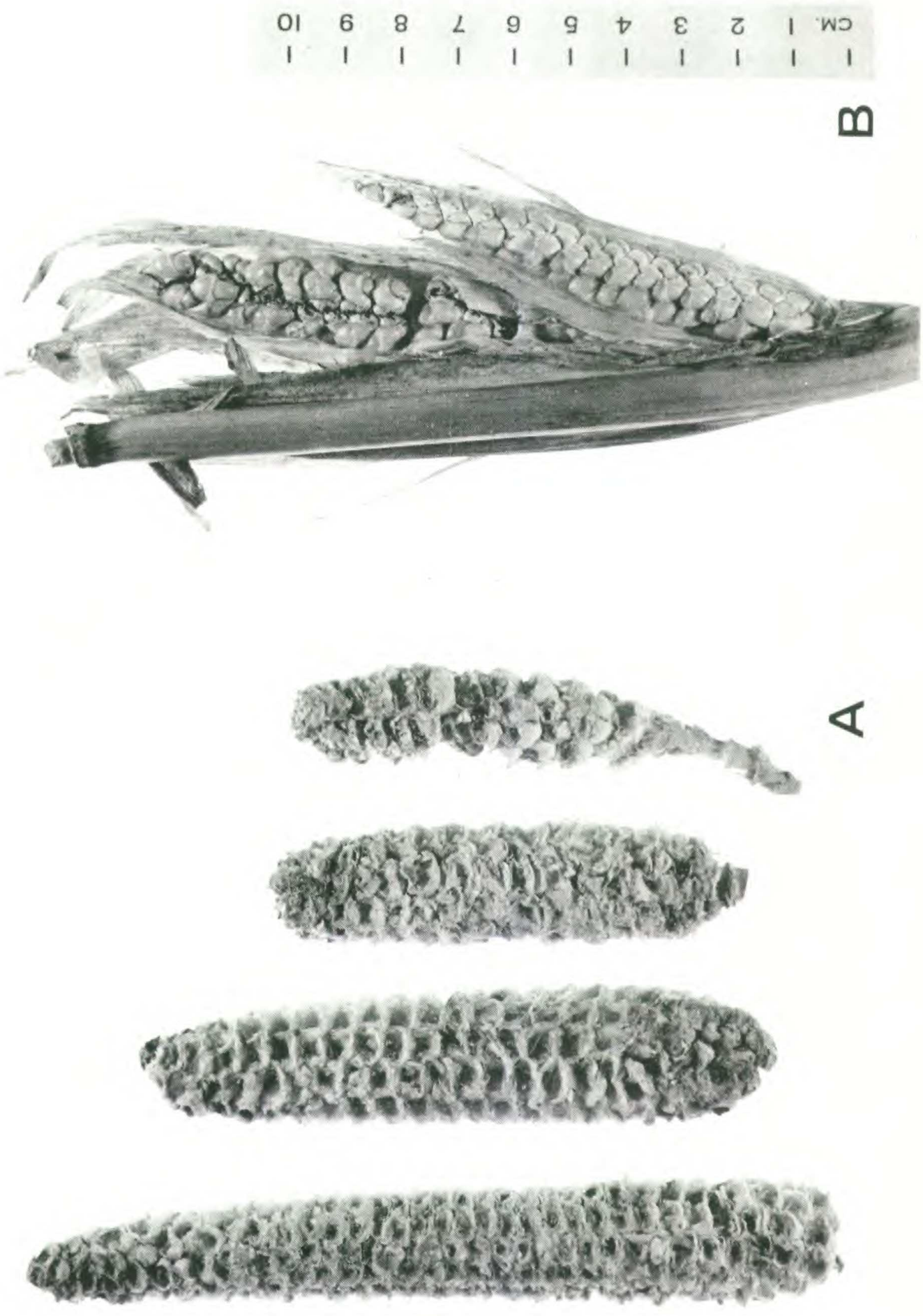


PLATE LXXVI. Evidence of teosinte introgression and maize × teosinte hybridization. A. The cob to the far left is a typical maize ear and shows evidence of introgression of tripsacoid segments associated with chromosome 9, and possibly chromosome 4. The cobs to the right are arranged in a series of increasingly pronounced tripsacoid characteristics. The extreme is the cob to the far right with its massive lower glumes and deep cupules. This cob, which was part of the maize harvest, is comparable in morphology to a maize backcross to the maize × teosinte hybrid. 7/10 actual size. B. This F_1 maize × teosinte hybrid came from the same field as the cobs in A. Note the two-ranked rachis, the paired spikelets, and the kernels forcing open the enclosing lower glumes; all typical characteristics of the F_1 hybrid. 7/10 actual size.

gy of the maize cob (Galinat et al., 1956; Sehgal, 1963). The presence of a short, thick rachilla inclined to the axis, pronounced glume cushions, slightly upcurved glumes, comparatively soft rachis tissue, and well developed central pith in the maize cobs of the fields suggests the introgression of segments of chromosome 9, and possibly chromosome 4, of teosinte.

Eight ears selected by the cultivator as seed ears from a field where maize×teosinte hybrids were known to be abundant were studied. These very productive ears were not highly tripsacoid, but they too showed evidence of teosinte introgression (rigid cob, straight rows, and indurated glumes). Four of these ears were shelled and 100 seeds from each ear were grown. Three cobs yielded all maize plants, but the fourth produced three maize×teosinte hybrids. This frequency of three maize×teosinte hybrids per 400 plants compares well with the number of maize×teosinte hybrids estimated to be present in the field and the abundance of highly tripsacoid cobs found in the total harvest.

Maize×teosinte hybrid seed on the predominantly maize-pollinated ear can not normally be distinguished morphologically from pure maize. Yet at Nobogame several ears from the same field were selected from the total pile because they possessed smaller than usual seeds. These small seeded ears uniformly yielded maize×teosinte hybrids when planted. It was found that if the ear is pollinated only by teosinte, the hybrid seeds are smaller than the few hybrid seeds found on a predominantly maize-pollinated ear. Thus there appears to be a chemical feed-back mechanism (growth hormone?) between the developing seed and the cob. This postulated hormone might act to stimulate the conduction of food through the cob to the developing seed.

Controlled pollinations of teosinte on the corn inbred

A158 have produced seeds which are smaller and weigh less than self pollinated A158. This phenomena is not universal because controlled pollinations of teosinte on the New England Flint, Wilburs Flint, produced hybrid seed which are indistinguishable in size and weight from self-pollinated Wilburs Flint.

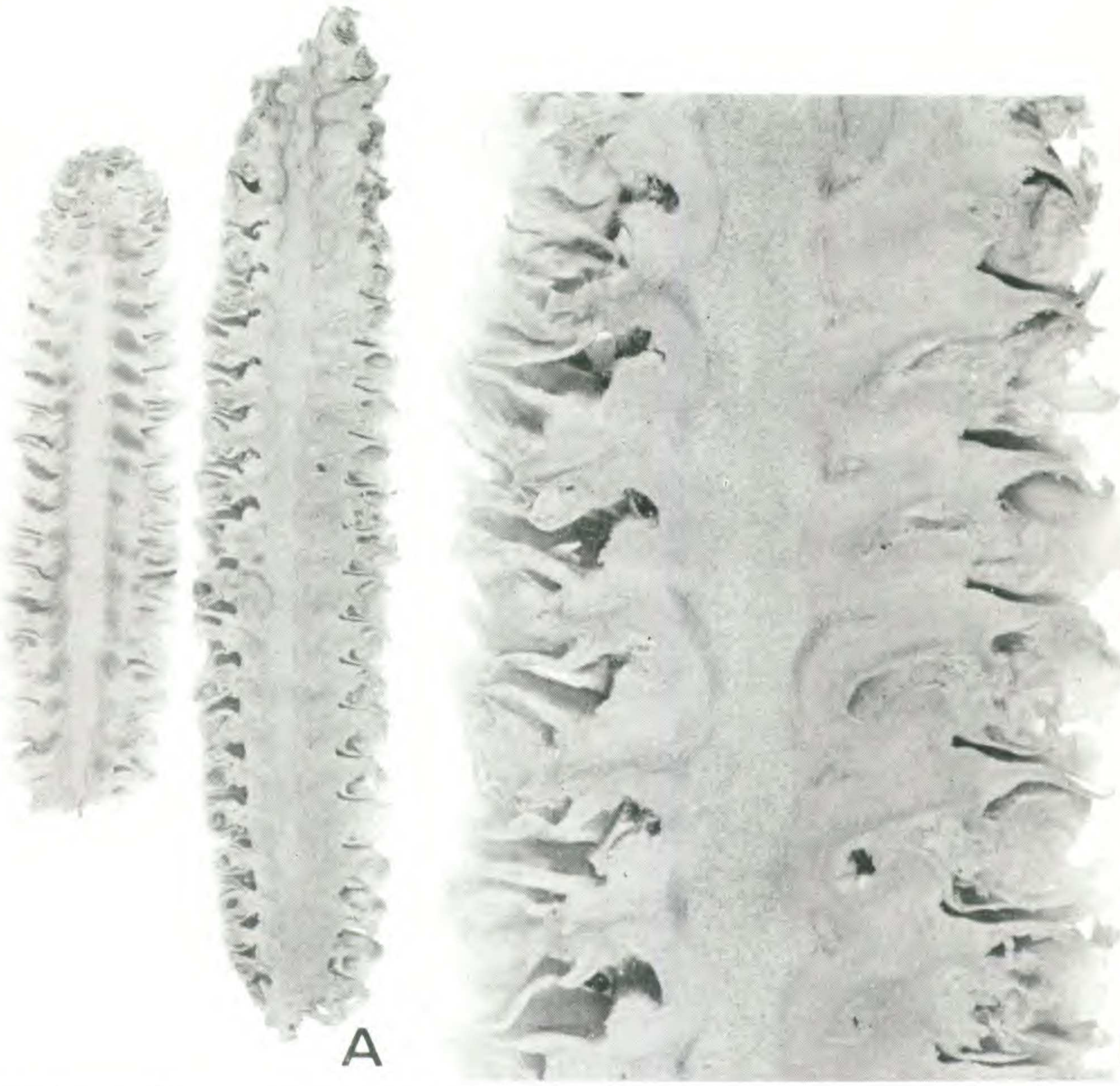
Discussion

Maize and teosinte are fully fertile, and in the Nobogame Valley the two hybridize naturally. Maize×teosinte hybrids are known from other regions in Mexico and Guatemala, but Nobogame is unique because hybrids are in some cases cultivated because the inhabitants feel they improve the maize and in others the hybrids are unknowingly planted in the maize fields.

Wild teosinte is abundant in the region, and hybrids are almost as abundant in the fields as on the margin of the fields. Because the method of cultivation of maize has not changed appreciably in the last hundred years this pattern of an abundance of teosinte hybrids on the seed ears is suspected to have been widespread in the past in regions where it is almost extinct today. Such a pattern of hybridization with teosinte would account for the widespread tripsacoid characteristics now found in the races of maize on the Central Plateau (Wellhausen et al., 1950) and adjacent regions. This hybridization in the past would also explain why the teosinte of the Central Plateau is one of the most maize-like races of teosinte.

The observations of the incorporation of teosinte segments from chromosome 9, and possibly 4, are interesting also because Sehgal (1963) has shown that, under experimental conditions, incorporation of teosinte chromosomes 9 and 4, either alone or in combination, in a uniform maize-inbred, increases the length of the cob. It is pos-

Plate LXXVII



Evidence of tripsacoid characters in Nobogame cobs. A. These maize cobs are from a typical field where hybridization with teosinte was known to occur. Actual size. B. The short, thick rachilla inclined to the axis, the slightly upcurved glumes, and the pronounced glume cushions suggest the introgression of tripsacoid segments on chromosome 9, and possibly chromosome 4, from teosinte. The rachis tissue is comparatively soft and the central pith is well developed. 3× actual size.

tulated that, since increased cob length is selected for in seed ears, teosinte hybridization is of positive selection value in the maize of Nobogame.

Summary

1. A detailed analysis of the maize fields was made in the Nobogame Valley in southwestern Chihuahua, where the pattern of cultivation for maize has not changed appreciably in the last one hundred years. The maize grown around Nobogame is a five month type belonging to the race Cristalino de Chihuahua. The teosinte belongs to the race Nobogame and is abundant along the margin of maize fields and growing wild in the non-cultivated parts of the valley.

2. Maize and teosinte are not seasonally isolated as they are at most other sites where the two occur together. The mid-flowering times overlap in August and maize ×teosinte hybrids occur naturally. Teosinte pollen is sufficiently abundant at flowering that many pollinations on maize cobs are by a teosinte parent. Seed ears of maize have been shown to be contaminated by teosinte pollen resulting in the actual planting of maize×teosinte hybrids by the cultivator.

3. The cobs of the maize planted in the valley show pronounced signs of tripsacoid germ plasm such as induration of the lower glume and a straight rigid cob. These characteristics are attributed to the introgression of tripsacoid genes via direct hybridization with teosinte followed by subsequent introgression from maize and teosinte backcross progeny. The maize backcross progeny are usually harvested while the teosinte backcross progeny are usually left standing in the field. Although introgression is reciprocal,

PLATE LXXVIII

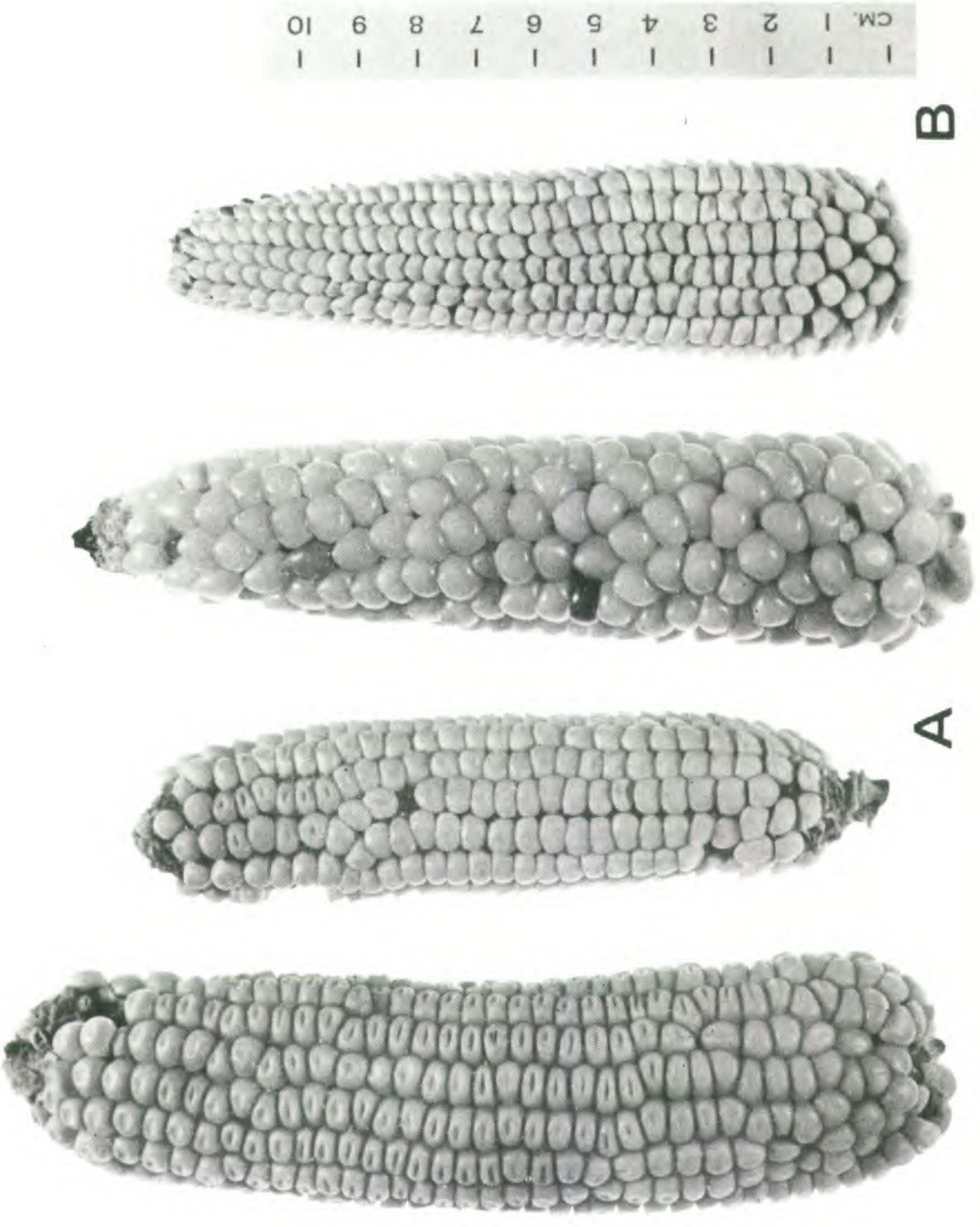


PLATE LXXVIII. Teosinte-pollinated maize ears. A. When the maize ear is pollinated only by teosinte, the hybrid seed are smaller than the few hybrid seed found on a predominantly maize pollinated ear, which are indistinguishable from the pure maize seed. The ear to the left is the inbred A158 and the ear to the right is a controlled pollination of teosinte pollen on the ear of A158. 7/10 actual size. B. These ears are open pollinated ears from Nobogame. The seed are of normal size on the ear to the left. The seed shelled from the ear to the right are smaller and all produced F_1 maize × teosinte hybrids. If the entire ear is pollinated by teosinte, none of the hybrid seed develop to the size of a normal maize kernel. This dwarfing effect only occurs if the entire ear is made up of hybrid kernels. Note also the tendency of the hybrid kernels to produce pointed seed, a character often found in pop corns. 7/10 actual size.

the main flow of genes appears to be from teosinte to maize, since the genetic incorporation of a maize-like rachis results in the inability to disperse seed and the extinction of these maize introgressed teosinte plants.

4. It is postulated that the hybridization of teosinte and maize on the Central Plateau in the past is comparable to the present hybridization of teosinte and maize at Nobogame. This hypothesis accounts for both the widespread presence of tripsacoid characteristics in the maize of the Central Plateau and the maizoid characteristics of the teosinte. The introgression of teosinte segments following maize×teosinte hybridization would have been of positive selection value if it resulted in a larger ear.

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